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## Abstract

Fallen flower bracts of the stilt-root palm, *Iriatea deltoidea,* impound up to five liters of rainwater in lowland Ecuador, and approximately one third of all falling bracts form an aquatic habitat. Although abundance of water-filled bract habitats varies greatly during the year, some bracts retain water up to four months. Over 450 fallen bracts were surveyed for their insect and anuran inhabitants during the course of two years in a lowland rainforest in eastern Ecuador. Insects from 10 orders and over 24 families were found utilizing bracts in some fashion. Of these, three orders and 10 families contained truly aquatic members. Two species of dendrobatids (Anura) were also found breeding in fallen bracts. Dipterous larvae, especially mosquitoes, were the most common insects. The presence of high numbers of dytiscid beetles makes this habitat unique among tropical phytotelmata. The size, abundance, and longevity of water-filled bract habitats, in conjunction with their rich fauna, suggest they are important phytotelmata habitats in eastern Ecuador, and their discrete nature makes them an ideal system for exploring many aspects of the biology of their inhabitants.


## Introduction

The use of plant held waters, or phytotelmata (*sensu* Varga 1928), by aquatic insects has attracted attention since an aquatic fauna associated with bromeliad leaf axils was first described by Müller (1879). Phytotelmata are bodies of water held by various plant parts including leaves, flowers, trunks, stems and fruit husks ( Varga 1928, Greeney 2001, Kitching 1971). Members of most major orders of aquatic insects have been found in phytotelmata, but the most prolific are dipteran larvae (Fish 1983, Greeney 2001), many of which are disease-vectoring species of mosquitoes (Downs & Pittendrigh 1946, Grimstad & Walker 1991, McClelland 1973, O'Connor 1923) or important pollinators (Entwistle 1972). The simple faunal associations, discrete nature, and abundance of phytotelmata habitats allow them to be examined on an individual basis as well as from a regional point of view, and provide excellent systems for studying ecological and community level processes (Fish & Beaver 1978, Kitching 2000, Maguire 1971).

Phytotelmata are traditionally broken into five or six major categories (Fish 1983, Greeney 2001, Kitching 1971, 2000), of which tree holes or stem holes are the most widespread, and found on almost every continent (Fish 1983). Pitcher plants in the families Sarraceniaceae and Nepenthaceae form a highly specialized aquatic habitat in both temperate and tropical regions (Beaver 1983), whereas leaf axil habitats are best known from tank bromeliad habitats (Frank 1983), which are mostly tropical in their distribution. Flower phytotelmata occur in various types of plants, but are best known in the genus *Heliconia* Linn. (Musaceae) (Seifert 1982). Fallen fruit phytotelmata have been well studied (eg. Caldwell 1992, Summers 1992), especially in *Theobroma cacao* Linn. (Sterculiaceae), whose fallen, water-filled fruits provide important breeding sites for pollinators (Soria *et al.* 1978). The sixth type of phytotelmata are fallen plant parts such as leaves or bracts, which have generally received little attention (but see Fincke 1998, Greeney 2001, Kitching 2000). Although mosquitoes occur in fallen bracts of several palm species in Venezuela, Panama, Costa Rica (Fincke 1998, Heinemann & Belkin 1977, 1978a, 1978b), Fiji (Paine 1943), and Brazil (Hutchings 1994), the other fauna has been largely ignored and never described detail.

The genus *Iriartea* Ruiz & Pav. (Palmae, Aracoideae, Iriarteeae) contains a single species (*I. deltoidea* Ruiz & Pav.) (Henderson *et al.* 1995) and is closely related to the genera *Dictyocaryum* H. Wendl., *Iriartella* H. Wendl., *Socratea* H. Karst., and *Wettinia* Poepp. ex Endl. All of these genera, including *Iriartea*, belong to the 'stilt root' group (Moore 1973) because the trunks arise from a cone-shaped mass of roots (Figure 1).

While several species of palms (Hutchings 1994, Greeney pers. obs.) and other plants such as *Cecropia* Loefl. spp. (Moraceae) (pers. obs.) produce flower bracts of adequate size and shape to collect water, none have been well studied. Additionally, within the vast body of phytotelmata literature, there is often confusion between the expanded leaf petioles of fallen palm leaves and the flower bracts described here. Bracts are often incorrectly referred to as fallen 'fronds' (eg. Fincke 1998), and it is often unclear as to which plant structure the author is referring (eg. Kitching 2000). While the semi-woody, inflated petioles of fallen palm fronds do often form phytotemata, the bract habitat described here is a much more prolific and important type of phytotelmata (pers. obs.). Here I provide the first detailed description of the fallen flower bract phytotelmata of *Iriartea deltoidea*, describe their diverse faunal assemblage in Ecuador, and demonstrate them to be an important phytotelmata habitat.

## Methods

### Study site

The majority of fieldwork was carried out from October 1996 to June 1998 at the La Selva Lodge Biological Station (LSBS) in the Sucumbios Province of north-eastern Ecuador. The station is located in a floodplain near the community of Anyañgu, 75 kilometers E.S.E. of Coca in an area between the Napo River and the oxbow lake, Mandi Cocha (0º 29' 50.3"S; 76º 22' 28.9"W). For a more thorough site description see DeVries *et al.* (1999) and DeVries and Walla (2001). Other observations were made at the Sacha Lodge Research Station (SLRS) located in similar habitat along the Napo River, ten kilometers west of LSBS.

## Study species

*Iriartea deltoidea* is entirely neo-tropical in its distribution, occurring from Nicaragua to Bolivia (Henderson 1990). It occurs from sea level up to 1300 meters in a variety of microhabitats, but is most common along stream margins and areas of flooded forest. It is common on the eastern slopes of the Andes below 1000 meters, and a frequent member of natural second growth after disruption of the canopy by the falling of large trees (pers. obs.). Other studies on *I. deltoidea* suggest that it is a specialist on small to medium sized light gaps in mature forests (Vandermeer *et al.* 1974). Schatz *et al.* (1985) suggest that it is the stilt roots of the Iriartinae that enable them to grow rapidly in light gap situations, and Losos (1995) suggests that a lack of natural seed dispersers restricts *I. deltoidea* to mature forests. Although *I. deltoidea* forms a significant portion of the forest canopy in some areas of western Ecuador (J. Clark pers. com.), at LSBS and SLRS most individuals have their crowns just below the canopy or in the mid-story (pers. obs.).

Despite the relatively slow growth of *I. deltoidea* (Vandermeer *et al.* 1974) and harvest by humans (Cerón & Montalvo 1998), these palms were common at both my study sites. Surveys by Balslev *et al.* (1987) and Korning *et al.* (1991), in a site only several kilometers from LSBS and SLRS, found *I. deltoidea* to be the most abundant tree, comprising 13 percent of trees over 10cm diameter at breast height (dbh).

## Field methods

To determine the seasonal abundance of bract habitats, 68 *I. deltoidea* trees over 19cm dbh were marked within the study area because trees of this size were expected to flower (pers. obs.). During the first week of every month the number of shed bracts was recorded for each tree. To access the percentage of bracts that naturally form phytotelmata, the number of bracts resting in a position that could collect water were recorded.

Because pH may affect faunal assemblages of phytotelmata (Fish & Carpenter 1982, Sota 1993), the pH of bract waters was measured from 63 individual bracts using a HACH Wide Range Indicator pH meter (No. 1470-11), sensitive to within pH 0.5. To determine the longevity of bract habitats, 28 newly fallen bracts were monitored at least weekly until they no longer held water. To approximate the density of *I. deltoidea* at LSBS, nineteen 100 square meter plots along a transect from the Napo River to Mandi Cocha were randomly chosen and surveyed for mature *I. deltoidea* trees (over 19cm dbh).

During this study I evaluated 585 naturally occurring bract habitats using three comparative measures. Volume was approximated by emptying the bract water into a measuring container or by visually estimating the volume to the nearest 25ml. For the purposes of this paper, bracts are lumped into three categories based on water volume: small (under 200ml), medium (200-975ml), and large ($\geq$1000ml). Cover refers to how much the bract curled or twisted over onto itself to hide any portion of the existing water. By looking directly down on the bract from above a bract was scored as: 1 when all water surface area was visible, 2 when more than half was visible, 3 when less than half was visible, and 4 when no water was visible. Bracts were ranked in age from 1 to 4 based on the amount of deterioration observed since being shed from the inflorescence. A bract was scored as 1 if still fresh and yellow inside, 2 if it was mostly light brown, 3 if dark brown but sturdy, and 4 if it was dark brown and beginning to soften.

To compare the relative size of *I. deltoidea* bract habitats to other types of phytotelmata, water volumes were measured by siphoning or dumping their contents into a container. In total, 30 *Heliconia* spp. bracts, 7 tree holes, 15 fallen leaves of various species, and 27 fruits of various species of plants including *Fevillia* Linn. (Cucurbitaceae), *Phytelephas* Ruiz & Pav. (Palmae), and *Theobroma* (Sterculiaceae) were measured.

The visible surface area (VSA) of water contained in each fallen bract was estimated by viewing the bract from directly above using a pre-measured circle with an area of 254cm$^2$ Each bract was placed in one of three VSA size groups (1=less than 254cm$^2$, 2=255 to 635cm$^2$, and 3=greater than 635cm$^2$).

To survey bract faunal assemblages, I examined the contents of 460 individual, naturally occurring bracts. The entire content of each bract was emptied into a zip-lock bag, returned to the field lab, and examined in a white tray. All insects were removed, placed into 70% EtOH, and retained for later identification. Larval anurans were identified in the field by raising them to adults.

## Results

During flower maturation up to sixteen bracts form a protective horn-shaped casing around the inflorescence (Henderson *et al.* 1995) (See Figure 1). After maturation of the inflorescence, bracts fall to the ground where they often fill with rainwater (Figure 2). The interior surface of fresh bracts is waxy yellow-white and, as they age, turns light brown and finally dark brown or nearly black. Bracts turn from yellow to light brown in 1-2 days and from light to dark brown in 2-3 days. After turning brown the bracts slowly soften and rot. Bracts often remain attached to the tree until well after they have begun to change color, and most fall while they are light brown. Bract phytotelmata can potentially occur in any combination of cover and age. The distributions of the various bract states are detailed in Table 1, which shows that most bracts in this study were of age 3 or 4 and had a cover of 1 or 2. In other words most were dark brown and a large portion of the water surface was visible from above.

Approximately 32% of fallen bracts accumulated rainwater (n=327). The majority of bracts were arc-shaped and split open along the inside of the arc such that they landed with a good chance of being in a position to impound water. Based on their size and position, bracts held up to 5 litres of water, with the average bract holding 300ml, and most bracts (89%) holding less than 1000mls. This is compared with volumetric measures of other phytotelmata in the area in Table 2. Surface area estimates showed that half (49%) of naturally occurring bracts had a visible surface area of less than $254cm^2$. Roughly a third (35%) had a surface area of between $255cm^2$ and $635cm^2$, and the remaining 16% had surface areas greater than $635cm^2$.

Once a bract accumulated water, various factors affected how long it remained a suitable habitat for aquatic organisms. When filled with an abundance of water, newly fallen bracts often tipped over as they settled into the leaf litter. As bracts aged and softened, sharp or protruding ground litter underneath the bract occasionally punctured the bottom, causing the water to drain. Large rains occasionally caused older bracts to fill until they collapsed outward. Periods of several days without rain often caused the ends of the bract to dry out and split, also causing the water to drain. During this study one bract was destroyed by a vertebrate animal, apparently foraging in or under the bract, and another bract was eaten by termites. Mean longevity of bract habitats was 45 days, and no bract lasted longer than four months.

In addition to rainwater, fallen bracts also accumulated detritus in the form of flowers, leaves, sticks, and bark. Approximately 15% of bract phytotelmata were formed directly below a palm's inflorescence and accumulated large quantities of fallen flowers. These bracts became eutrophic, semi-aqueous habitats that appeared to recruit a different fauna that was characterized by the presence of large numbers of hover fly larvae (Syrphidae). In addition to plant material, most bracts accumulated numerous drowned insects including ants, orthopterans, coleopteran adults and larvae, heteropterans, and spiders.

The pH of bract waters ranged from 6.0 to 8.0, with the average bract pH being 7.0. Younger bracts (age classes 1 and 2) had an average pH of 6.9 (STDEV=0.55) and older bracts (age classes 3 and 4) averaged 7.3 (STDEV=0.34). These differences in Ph differed significantly (one-tailed T-test $p=0.001$).

At LSBS mature *I. deltoidea* trees occurred in densities of approximately 79 trees per square kilometer, and not all sampled trees flowered. However, the 50 trees that flowered at least once produced, in total, between 55 and 70 fallen bracts per month from September to December. From January to August, they produced only 5 to 18 bracts per month, with February, March, and April being the lowest months. On average, each flowering tree produced 6.6 (STDEV=4.0) bracts and the average for all trees over 19cm dbh was 0.48 (STDEV=4.5) bracts per tree.

The average number of bracts produced per tree (all trees over 19cm in diameter included) during the most productive months (October, November, December) multiplied by the estimated number of trees per square kilometer produces 71 fallen bracts per square kilometer per month. If 32% of the total fallen bracts per month form phytotelmata habitats I estimate there were 23 water filled bracts per square kilometer, per month, representing an aquatic habitat volume of approximately 6.9 litres of bract habitat per square kilometer during the most bract-rich months. During the lowest bract production months (February, March, and April) I estimate an aquatic habitat volume of approximately 2.7 litres per square kilometer. I have observed, however, that some bracts can last as long as 120 days and would therefore still be present during months in which few new bracts are produced. Totaling the calculated volume per square kilometer for all months of a year, I estimate 36.6 litres of aquatic bract habitat created per year per square kilometer.

Insects representing 10 orders and at least 24 families were found utilizing bracts in some fashion. Of these, three orders and ten families included truly aquatic species (See Tables 3 and 4 for a summary of insect fauna).

Aquatic and semi-aquatic insects associated with bracts

CULICIDAE (Diptera): Larval mosquitoes were by far the most numerous insects encountered. Approximately 81% of bracts contained at least one species of mosquito. Some bracts contained almost 1 larva per milliliter. Four species were raised from bract waters. At least one of these, *Toxorhynchites* sp., was found to be predaceous. *Toxorhynchites* larvae occurred in 25% of naturally occurring bracts, but were never encountered in densities exceeding 13 individuals per bract. Observations showed these larvae to be voracious predators of other mosquitoes, tadpoles, chironomid larvae, and each other.

SYRPHIDAE (Diptera): One species of syrphid was raised from bract waters. Syrphid larvae were found in only five percent of bracts, but when encountered, were usually quite numerous (7-63 individuals per bract). On one occasion, over 60 adults were raised from a single bract containing only 300mL of water. These larvae appear to be detritovores and were seen to move about the bottom of bracts, presumably grazing phytoplankton from the bract wall and from accumulated debris. They appear to prefer older bracts containing large amounts of fleshy plant parts and dead insects. Additionally, they are most often associated with shallower bracts, which possibly allow them to feed while still respiring through their anal siphon. Larvae placed in water over three centimeters deep in the laboratory quickly died, while those in shallower water survived to pupation. Pupation occurred in leaf litter away from the bract.

CHIRONOMIDAE (Diptera): Due to the minute nature of these flies, they were often hard to locate under field conditions and only about 50 bracts were effectively surveyed for their presence. Of these, 45% contained chironomid larvae. They were most often encountered in older bracts with more detritus in the bottom.

DYTISCIDAE (Coleptera): Fourteen species of adult dytiscids were found in bracts during the course of this study. *Laccophilous* sp. was encountered only twice, two individuals of *Desmopachria* sp. were found in one bract, and three individuals of *Thermonectes* sp. were found in an experimental bract located in a highly disturbed area dominated by bamboo (*Guadua* sp.). Both

*Laccophilous* sp. and *Desmopachria* sp. were also observed in small, rain-fed streams within the forest, but were most common in temporary pools created in the root divots of wind-thrown trees. Both of these species were also attracted to dark green artificial containers filled with water. *Thermonectes* sp. was only encountered in these wind-thrown tree pools.

By far the most common dytiscids were those in the genus *Copelatus*. Over 1000 *Copelatus* were collected during the course of this study. The taxonomy of these beetles is uncertain, and many of the species collected are undescribed (Roughley pers. comm.) Temporarily, the *Copelatus* collected in this study have been separated into 13 species based on gross morphological characters (Greeney 1999). *Copelatus* spp. occurred in 47 percent of bracts surveyed, and commonly reached densities of over 15 beetles per bract. One bract contained 111 individuals, and had a density of one dytiscid for every three milliliters of water. *Copelatus* sp.#1, *Copelatus* sp.#9, and *Copelatus undecimlineata* were the most common, and accounted for 63% of the individuals collected. *Copelatus* sp.# 11 was collected from only one bract where five individuals were found. These *Copelatus* spp. were only found in bracts, pools formed in the divots created by wind-thrown trees, fallen leaves, and water-filled footprints in forest paths. None were ever encountered in flowing water or still water connected to flowing water.

HYDROPHILIDAE (Coleptera): Six species of hydrophilids were encountered in bracts. All were adults, and no larvae were ever found. Of the six species, *Hydrobiomorpha* sp. was encountered only once in the same bract that contained the three *Thermonectes* sp., and *Enochrus* sp. was found in only one bract. *Derallus sp.*, occurred in bracts only rarely (<10 bracts), and the three *Pelosoma* spp. were found in fewer than 20 bracts. At least two other species of *Pelosoma* were collected from similar phytotelmata in the area, and as this is a problematic genus (Hansen pers. comm.), it is likely that as bracts are better studied, more species will turn up. *Derallus* sp. was frequently found in small rain-fed streams and in wind-thrown tree pools. It was also frequently found in experimental, water-filled, dark green, rubber tubs (Greeney unpubl. data). No frequency data was collected for any of these, but *Dactylosternum* sp. was often found in bracts and occasionally reached densities of nearly 30 individuals per bract. Except for *Enochrus* sp. and *Hydrobiomorpha* sp., all bract inhabiting hydrophilids appeared to live between the fibrous layers of rotting bract walls and amongst the detritus near the edge of the water.

NOTERIDAE AND NOSODENDRIDAE (Coleptera): Only one specimen of *Notomicrus* sp. and one specimen of an undetermined nosodendrid were collected from bracts. Their extremely small size, and ability to disappear into small cracks in pieces of debris, however, may have led to them being overlooked on other occasions.

VELIIDAE (Hemiptera): One species of veliid (*Microvelia* sp.) was collected from fallen bracts during the course of this study. One bract contained two immatures, and three other separate bracts contained one adult each. This is a genus normally associated with bromeliad waters (Distant 1912, Drake & Harris 1935, Drake & Hussey 1954), and the species found in bracts may not be specific to bract habitats.

CORIXIDAE (Hemiptera): One immature corixid was found in an experimental bract located near a small stream. It was collected after recent rains had caused the stream to overflow and wash out the contents of many bracts. It is probable that the corixid was washed into the bract from the stream during this flood.

HYDROMETRIDAE (Hemiptera): One immature hydrometrid was also collected on the water surface of a bract located near where the corixid was found. This individual was also most likely washed in during the same flood.

GOMPHIDAE (Odonata): One immature gomphid was found in a bract also located near a small stream. No recent floods had occurred, so it is possible that the insect was oviposited there accidentally by a normally riverine species. The small size of the nymph prevented positive identification, but it is suspected to be a member of the genus *Aphylla*.

Terrestrial or amphibious insects associated bracts

All of the following records are of insects normally considered to be terrestrial. Many appear to enter bract waters to feed on living or dying aquatic organisms, or to scavenge rotting plant or animal matter. Until the ecology of phytotelmata inhabitants is better understood, however, few species found in these habitats should be discounted as strictly terrestrial, and some of the terrestrial species surely impact the aquatic inhabitants in some fashion.

STAPHYLINIDAE (Coleoptera): At least two species of staphylinids were frequently found in and around bract habitats. I observed them preying on mosquito larvae near the water's edge, and they were frequently found in drying bracts. In these drying bracts they preyed on dying mosquito larvae and tadpoles. They were most frequently found in older more rotten bracts.

CARABIDAE (Coleoptera): Carabid beetles were also occasionally seen inside bracts behaving in a manner similar to staphylinids.

SCOLIIDAE (Coleoptera): Scoliid beetles were often found struggling on the water's surface where they apparently became trapped after emerging from the non-aquatic sections of the bract. When bracts are torn apart, numerous individuals were found, and it is presumed they feed upon the structure of the bract and are non-aquatic.

SCARABAEIDAE (Coleoptera): Three species of dung beetles were found apparently foraging on accumulated plant matter in fallen bracts. *Eurysternus confusus* was the most frequently found, with 7 individuals from 5 different bracts. *Canthidium* sp. was found in one bract, and *Uroxys* sp. was found in three separate bracts. All of these beetles were collected from older bracts filled with fallen flower parts. As with *Bdelyrus* dung beetles, often collected in bromeliads (Cook 1998), it is thought that these species were feeding on the decaying vegetable matter within the bracts, and are not truly aquatic.

FORMICIDAE (Hymenoptera): On numerous occasions, ants of various species were seen foraging in and around bracts. As a bract begins to dry up and the aquatic fly larvae within are exposed, many species of ants were observed feeding on the helpless larvae. Particularly common were species of *Odontomachus* and *Solenopsis*. One species of attine (*Apterostigma* sp.) was twice found to nest in overturned bracts.

ISOPTERA: Termites in the common neotropical genus *Nausititermes* were occasionally found feeding upon the woody structure of fallen bracts. While not aquatic, their destruction of the bracts' physical integrity most certainly impacts the aquatic species within.

DERMAPTERA: At least two species of dermapterans were found in bracts of all ages behaving in a manner similar to that described for staphylinids and carabids.

ORTHOPTERA and BLATTODEA: As many bracts curl over upon themselves to form small dark crevices or overhangs, they form ideal diurnal refugia for nocturnal insects such as cockroaches, katydids, and crickets. These crevices were frequently inhabited by more than one individual.

COLLEMBOLA: Collembolans were frequently found on the water's surface inside bracts. As they did not appear well adapted for this environment, it is assumed that they fell or jumped there accidentally when disturbed from the surrounding leaf litter. On several occasions, however, numerous individuals were seen aggregated along the margin of the bract water, and collembolans were often very numerous in rot-filled bracts such as those inhabited by syprhids and dung beetles.

## Non-insect inhabitants of fallen bracts

In addition to many species of spiders seen incidentally foraging in and around bracts, phalcid spiders were frequently found spinning webs inside bracts. They presumably fed upon emerging aquatic insects or those arriving to oviposit.

Many species of amphibians were also found in bracts. On one occasion a juvenile salamander (*Bolitoglossa peruviana)* was found outside the water buried in moist detritus. Other amphibian adults seen in bracts in the field include the anuran species *Epipidobates bilinguous, Colostethes marchesianas, Eluthrodactylus lanthanoides* Dendrobatidae), *Bufo tiphonius* (Bufonidae), and *Hyla granosa* (Hylidae). *Epipidobates femoralis*, however, was by far the most common adult frog seen in bracts. Two of these frogs, *C. marchesianas* and *E. femoralis* were found to frequently breed in bracts. Twenty-seven percent of water filled bracts were found to contain at least one tadpole, with densities in some bracts reaching over 30 individuals. Those species not found to breed in bracts are assumed to be foraging there, and on one occasion, an individual *B. tiphonius* was seen eating tadpoles contained in a bract.

## Discussion

This study indicates that the shape of fallen palm bracts produces a fairly high water surface area-to-volume ratio. Of other described phytotelmata habitats present in this region, bracts are probably most similar to 'pan' or 'crack' type tree holes (Kitching 1971). Holes in vertical trunks, leaf axils, and flower bracts are all shaped in such a way as to have relatively high volumes with little or no water visible from above. For animals searching for aquatic habitats by visual means, such as coleopterans and heteropterans (Fernando 1958, 1959, Schwind 1991), this trait would make *Iriartea* bracts relatively more apparent. This is supported by the unusually high number of aquatic beetle species associated with *I. deltoidea* bracts.

Although not measured directly at LSBS, previous estimates of bromeliad water volumes indicate that they may hold substantially more water than *Iriartea* bracts (Picado 1913, Sugden & Robins 1979). While tree holes are not as common as *Iriartea* bracts at LSBS, they hold substantially more water per tree hole. Several studies suggest that tree hole habitats persist much longer than bract habitats (Fincke 1998, Kitching 1983, Lounibos 1983), and may be a more stable, and volumetrically larger, aquatic habitat. In contrast, I found that fallen fruits, especially *Fevillia* (Cucurbitaceae), were common at LSBS, but they held less water than the average *I. deltoidea* bract. In a similar fashion *Heliconia* flower bracts were abundant at times, but the total volume of all bracts on an individual inflorescence held substantially less water than the average *Iriartea* bract. My volumetric estimates suggest that fallen bracts of *I. deltoidea* represented a substantial proportion of the phytotelmata habitat at my study site, and likely in other lowland tropical rainforests.

The frequent occurrence of rotting flower parts and drowned insects, and the fleshy or woody nature of bracts caused them to often smell like sewage or feces. This characteristic makes bracts similar to fallen fruit husks that often contain rotting flesh of the fruit as well as water. The odor and chemical composition of phytotelmata habitats may play an important role in habitat selection for many mosquito species (Hudson & McLintock 1967, Istock *et al.* 1983, Kalpage & Brust 1973, Lounibos 1978, Lounibos & Machado-Allison 1993). The pH of phytotelmata may also be important in habitat selection, especially by mosquitoes (Fish & Carpenter 1982, Sota 1993).

I found that bract waters in Ecuador were slightly more basic than water contained in tree holes, leaf axils, and bracts in other studies (ie. Fincke 1998, Kitching 1983, Torales *et al.* 1972, Winder 1977), but similar in pH to *Heliconia* flower bracts (Machado-Allison *et al.* 1983) and to tree holes in Panama (Fincke 1998). The combination of a generally higher pH and strong odor may be important olfactory and chemical cues to phytotelmata colonizers that use *I. deltoidea* bracts.

The ease with which *I. deltoidea* bracts can be surveyed and their broad geographic distribution makes them ideal for studies on community structure, faunal interactions, and habitat selection. In particular, *I. deltoidea* bract communities are ideally suited for experimental studies of aquatic communities that have traditionally been conducted on phytotelmata habitats such as tree-holes, which are less easily completely surveyed and spatially manipulated. (Fincke 1999, Fincke *et al.* 1997, Kitching 1971, 1987, 1990, Yanoviak 1999a, 1999b). It is my hope that this study will serve to introduce *I. deltoidea* bracts as important Neotropical phytotelmata, and provide a platform from which further studies may be undertaken.

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| | Age 1 | Age 2 | Age 3 | Age 4 |
|---|---|---|---|---|
| Cover 1 | 2 | 4 | 3 | 1 |
| Cover 2 | 12 | 4 | 8 | 0 |
| Cover 3 | **173** | **83** | 39 | 21 |
| Cover 4 | **69** | **62** | **74** | 30 |

**TABLE 1** Distributions of bract morphology. The relative abundance of bracts with cover ratings 1-4 in the left column and age ratings 1-4 across the top are shown here. The numbers indicate those bracts with that pair of characteristics. The samples in bold are those bracts which represent 79% of the total bracts examined.

| Phytotelmata type | Average volume (ml) |
|---|---|
| Fruit husks | 87 (n=27) |
| *Heliconia* bracts | 18 (n=30) |
| Tree holes | 1186 (n=7) |
| Fallen leaves | 86 (n=15) |
| *Iriartea* bracts | 300 (n=585) |

**TABLE 2** Average water volumes contained by phytotelmata at LSBS. Average volumes measured at La Selva, Ecuador are given in column 3.

| Family | Species | Occurrence |
|---|---|---|
| Culicidae | *Toxorhynchities* sp. | R |
| Culicidae | | R |
| Culicidae | | R |
| Culicidae | | R |
| Syrphidae | | R |
| Chironomidae | | R |
| Dytiscidae | *Copelatus* sp.#1 | R |
| Dytiscidae | *Copelatus* sp.#2 | R |
| Dytiscidae | *Copelatus* sp.#3 | R |
| Dytiscidae | *Copelatus* sp.#4 | R |
| Dytiscidae | *Copelatus* sp.#5 | O |
| Dytiscidae | *Copelatus undecimlineata* | R |
| Dytiscidae | *Copelatus* sp.#7 | R |
| Dytiscidae | *Copelatus* sp.#8 | R |
| Dytiscidae | *Copelatus* sp.#9 | R |
| Dytiscidae | *Copelatus* sp.#10 | R |
| Dytiscidae | *Copelatus* sp.#11 | O |
| Dytiscidae | *Thermonectes* sp. | A |
| Dytiscidae | *Desmopachria* sp. | A |
| Dytiscidae | *Laccophilous* sp. | A |
| Hydrophilidae | *Hydrobiomorpha* sp. | A |
| Hydrophilidae | *Enochrus* sp. | O |
| Hydrophilidae | *Derallus* sp. | R |
| Hydrophilidae | *Pelosoma* sp.#1 | R |
| Hydrophilidae | *Pelosoma* sp.#2 | R |
| Hydrophilidae | *Pelosoma* sp.#3 | R |
| Nosodendridae | | A? |
| Noteridae | *Notomicrus* | A? |
| Veliidae | *Microvelia* sp. | O |
| Hydrometridae | | A |
| Corixidae | | A |
| Gomphidae | *Aphylla*? sp. | A |

**TABLE 3** Aquatic or semi-aquatic insects found in bracts. Occurrence of each species is noted as regular (R), occasional (O), of accidental (A). Insects labeled R were found in at least 15 bracts, those labeled O were found in less then 15 bracts, and those labeled A are those thought to have been accidental invasions of bract habitat.

| Family or Order | Species | Occurrence |
|---|---|---|
| Staphylinidae | Various | R |
| Carabidae | Various | R |
| Scolyidae | Various | R |
| Scarabaeidae | *Eurysternus confusus* | O |
| Scarabaeidae | *Canthidium* sp. | O |
| Scarabaeidae | *Uroxys* sp. | O |
| Tettigoniidae | Various | R |
| Gryllidae | Various | R |
| Blattodea | Various | R |
| Collembola | Various | R |
| Dermaptera | Various | R |
| Isoptera | *Nausutitermes* sp. | O |
| Formicidae | *Odontomachus* spp. | R |
| Formicidae | *Solenopsis* spp. | R |
| Formicidae | *Apterostigma* sp. | O |

**TABLE 4** Terrestrial or amphibious insects found in bracts. Occurrence of each species is noted as regular (R), occasional (O), or accidental (A). Insects labeled R were found in at least 15 bracts, those labeled O were found in less then 15 bracts, and those labeled A are those thought to have been accidental invasions of bract habitat.

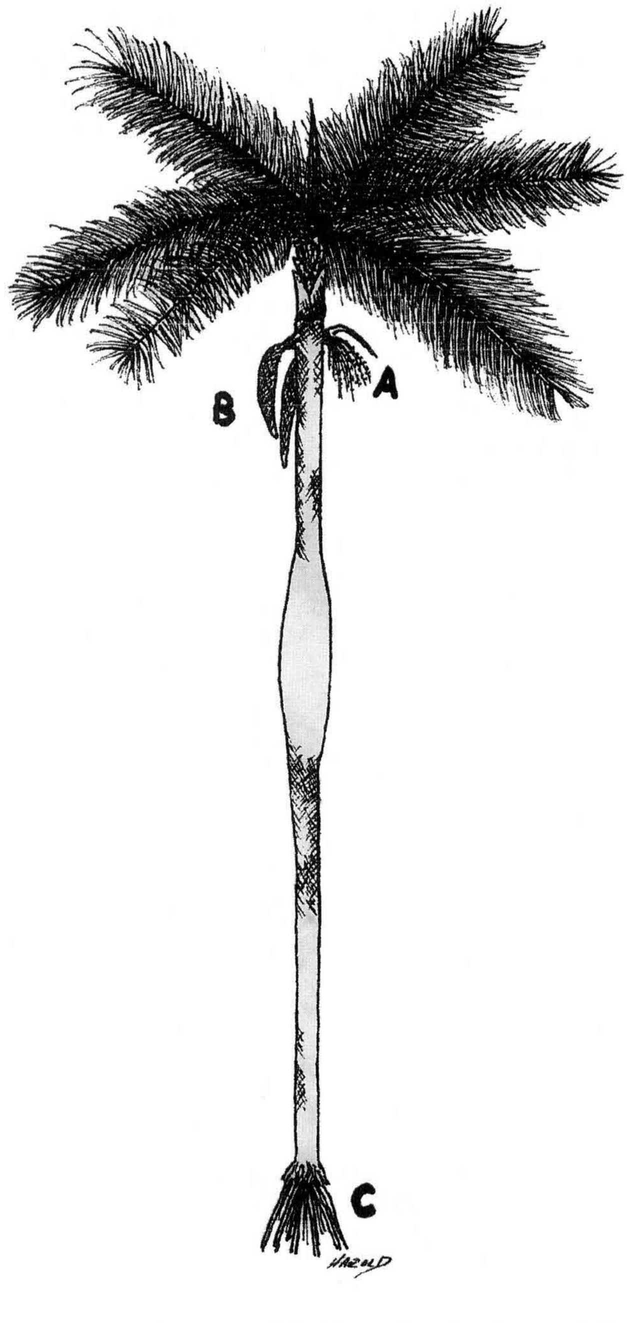


**FIGURE 1** Mature *Iriatea deltoidea* palm showing an infructescence (A), an immature inflorescence before flowering and with bracts still in position (B), and the typical stilt-roots (C).

**FIGURE 2** Fallen flower bract forming a phytotelmata A typical phytotelmata habitat formed inside a fallen *I. deltoidea* flower bract. The example shown here is of cover rating 2 and age rating 3. It is holding approximately 300ml of water.